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Hollenbeck, A. C., & Palazotto, A. N. (2012). Methods Used to Evaluate the Hawkmoth (*Manduca Sexta*) as a Flapping-Wing Micro Air Vehicle. *International Journal of Micro Air Vehicles*, 4(2), 119–132.  
<https://doi.org/10.1260/1756-8293.4.2.119>

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# Methods Used to Evaluate the Hawkmoth (*Manduca Sexta*) as a Flapping-Wing Micro Air Vehicle

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Received 10 April 2012, Accepted 28 May 2012

## ABSTRACT

Examining a biological flapping-flight mechanism as a mechanical system provides valuable insight related to the development and construction of Flapping-Wing Micro Air Vehicles (FWMAVs). Insects provide excellent candidates for this reverse-engineering, and one species in particular, the hawkmoth *Manduca sexta*, stands out as an exceptional model. Engineers with FWMAV aspirations can benefit greatly from knowledge of *M.sexta*'s advanced yet deceptively simple flight mechanism. Avenues for investigating this mechanism include finite element modeling, nanoindentation for material properties, and mechanical power output calculations or measurement. This paper presents these concepts and reviews existing literature to provide a platform for ongoing FWMAV research and design.

## 1. INTRODUCTION

Very small, autonomous, and agile MAVs with hovering capability are desirable for military and civilian applications. These flying robots, which will almost certainly require flapping wings to meet the hovering requirement, will be useful for gathering information in nearly any dangerous scenario which precludes direct human participation. For example, a FWMAV equipped with air-quality sensors could enter a contaminated building or area, enabling rescuers to determine the nature of the contaminant and whether it is or when it will be safe to enter. [3, 4, 6].

*M.sexta*'s thorax/wing structure can be modeled as a mechanical spring system (Fig. 1). Loads applied to the thorax by the flight muscles cause compression which in turn moves the wings through hinges on either side of the thorax. Relating force and compression yields energy, or work done. Data of this type furthers the understanding of this biological organism from a mechanical standpoint, and provides a basis to which current and future FWMAVs can be compared.

The mechanical power output of this system can be found if the time during which this force and compression take place is known. It is well-known that flapping flight, especially in the low Reynolds conditions that *M.sexta* and FWMAVs experience [1], is "energetically demanding" and requires a very high power density [2]. This constitutes a challenge to engineers searching for micro power sources and delivery mechanisms for FWMAVs. Understanding the power density of the flight muscles of insects like *M.sexta* provides a much-needed benchmark which engineers can aspire to meet or surpass with their own power sources.

Cuticle, the material which comprises the plates of the insect exoskeleton, plays a significant role in the performance of this flapping mechanism. Examining the material properties of these flexible, possibly energy-storing components will be key for future FWMAV technological advances. The elastic modulus of the thoracic cuticle of *M.sexta* will serve as a benchmark to which synthetic materials, potential FWMAV components, might be compared. Tensile tests can divulge the elastic modulus of the cuticle, but nanoindentation is a simpler and non-destructive approach which yields the same results. The latter is a small-scale version of the standard indentation test, is normally used on thin-films or membranes of inorganic materials (metals, manmade composites, etc.) However, the method can also be applied to insect cuticle and other biological materials. In this paper, the science and history of nanoindentation of biological materials is summarized as it relates to engineering applications.

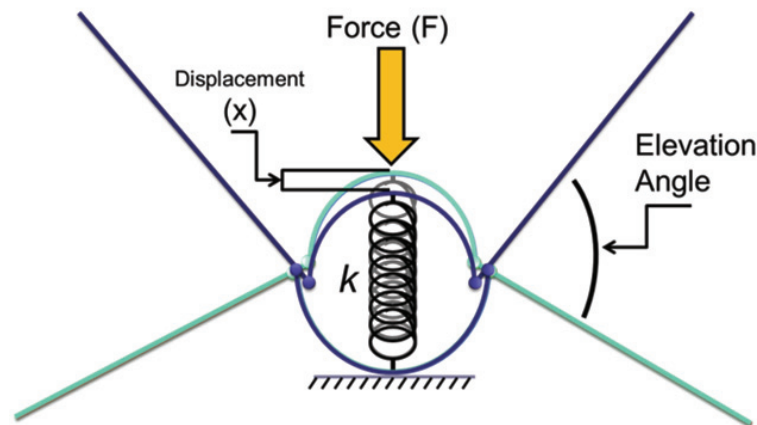


Fig. 1. Simplified mechanical model of *M.sexta* thorax/wing mechanism. More intricate models include the addition of a damper [17,25]

## 2. BIOLOGICAL INSPIRATION

A conventional approach to aircraft design, where subsystems are secondarily fitted inside a predetermined airframe, is not currently viable in the emerging and complex world of MAVs. These miniscule flying machines require fast-response controls, integrated lift and propulsion devices, flexible structures and micro-machinery, all of which must operate in low Reynolds aerodynamics [7].

Biological organisms are usually optimized under a broad range of constraints that might not necessarily apply to an engineered device with very specific requirements. For example, the wings of *M.sexta* are likely not optimally designed for maximum lift under a specific flight regime. Instead, the shape and size of these wings are the result of compromise between the requirements of hovering flight, evasive maneuvers, forward flight and takeoff. The structure of the wings is also limited by their development within the pupa casing and their need to unfurl and harden upon eclosion.

A biological organism, therefore, should not be reverse-engineered with intent to duplicate all of its functions. Instead, engineers involved in biomimetics should approach this problem with the understanding that their design constraints are often less demanding, or at least more specific, than those of nature, which enables deviations from the way the organism is designed. With this in mind, the goal of engineers in the FWMAV field is not to create a mechanical analog of *M.sexta* or some other insect. Instead, the aim is to characterize the design and functions of a species in order to apply that knowledge toward a well-tailored solution for the specific design problem. The approach to this characterization may then be generalized for any flapping-wing insect species, such as dragonflies, butterflies or bumblebees, in order to further increase the knowledge base of natural FWMAV technology.

### 2.1 Flapping Wings

Small, lightweight aircraft traveling at low speed experience very unstable conditions. An aircraft which weighs merely a few ounces does not have significant inertia, so even a slight wind gust can trigger relatively large forces and changes in momentum [8]. Highly sensitive flight control systems are required to maintain stability at such low Reynolds number conditions. Ifju has successfully shown that it is possible to overcome some instability issues, such as wind gusts, with fixed but flexible wings using bio-inspired adaptive washout (analogous to the rigid but flexible wings of a gliding bird) on his propeller-driven MAVs [9]. However, the dual challenges of providing low speed stability *and* producing propulsive thrust are solved simultaneously in nature each time an insect or a bird flaps its wings to get airborne:

“Interestingly, nature’s flyers of the same scale [less than 15cm] use another source of unsteady aerodynamics, flapping wings, to create both lift and propulsive thrust.” [5]

There are currently many bio-inspired FWMAVs in various stages of development. Some are already capable of self-powered, semi-autonomous flight. Wright State University has created at least 8 different FWMAVs between 2009 and 2011, having studied the kinematics of dragonflies (Fig. 2.a),

cicadas, butterflies, and ladybugs [10]. Some of their MAVs are capable of flying for up to 20 minutes at a time, and a few have carried small cameras.

The Harvard Microrobotics Laboratory has been in existence since 2000. Their research consists of soft actuators, sensors, ambulatory microrobots, and flapping-wing microrobots, or FWMAVs. They have had many successes in these areas, including the design and construction of the bee-inspired flier shown in Fig 2.b [11]. Another of their devices, modeled after a fly, achieved the first lift-off of a biologically-inspired at-scale FWMAV in 2008 [47].

AeroVironment, Inc., an engineering company which has had successes in a diverse range of challenging design problems, is developing a hummingbird-inspired FWMAV (Fig. 2.c). They were awarded a Phase II contract extension for their “nano” air vehicle development program by DARPA in 2009 [12], and have since met or exceeded all of the technical milestones, which are [13]:

1. Demonstrate precision hover flight.
2. Demonstrate hover stability in a wind gust flight which required the aircraft to hover and tolerate a two-meter per second (five miles per hour) wind gust from the side, without drifting downwind more than one meter.
3. Demonstrate a continuous hover endurance of eight minutes with no external power source.
4. Fly and demonstrate controlled, transition flight from hover to 11 miles per hour fast forward flight and back to hover flight.
5. Demonstrate flying from outdoors to indoors, and back outdoors through a normal-size doorway.
6. Demonstrate flying indoors ‘heads-down’ where the pilot operates the aircraft only looking at the live video image stream from the aircraft, without looking at or hearing the aircraft directly.
7. Fly the aircraft in hover and fast forward flight with bird-shaped body and bird-shaped wings.

This hummingbird FWMAV was named among the “50 Best Inventions of 2011” by Time Magazine in its inventions issue [14]. Its picture was featured on the cover of that issue, indicating that people really are becoming more aware of and interested in this technology [15].

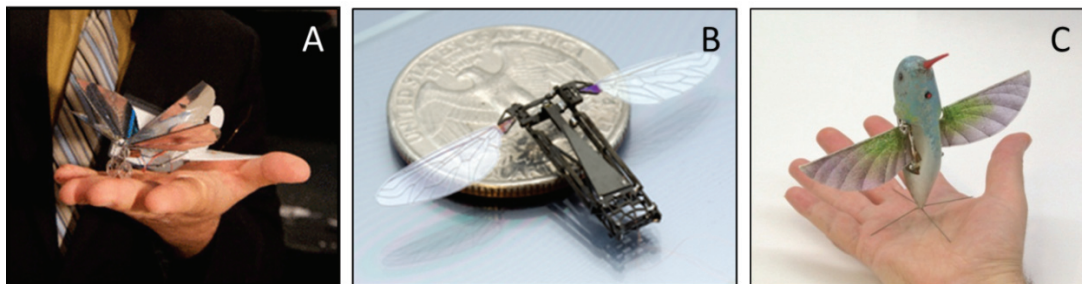


Fig. 2. Examples of current FWMAV technology: (A) Wright State's dragonfly [10], (B) Harvard's monolithic bee [11], (C) AeroVironment's hummingbird [13]

### 3. WHY *MANDUCA SEXTA*?

Many flying insects exhibit the type of hovering agility necessary for FWMAVs. While hummingbirds and bats are also capable of true hovering flight, insects like *M.sexta* are closer to the target size range for MAVs. Because they are naturally adept at hovering in place during feeding even in gusty conditions, hawkmoths display a remarkable ability to hover in small, enclosed spaces, making them an excellent model for FWMAVs with high degrees of stability and control [16]. This insect is also an efficient flier known for long-lasting flight [20]. In addition, only insects possess an exoskeleton with elastic proteins (called resilin) which enable the entire thorax to function as a mechanical spring-damper system capable of efficiently operating at resonance during flapping flight [17]. *M.sexta* stands out among the flying insects for its large size and relatively simple design. A member of the moth family *Sphingidae* and Hawkmoth genus *Manduca*, this species is designated *sexta* for the six pairs of orange dots on the abdomen (Fig. 3.a) [18], and is often referred to by the common name Tobacco Hornworm Moth. They are easy to rear (see Appendix A), readily available in the wild, and provide a suitable platform from which to study a basic flying insect. Their flight motor system consists of a

simple arrangement of two sets of massive flight muscles which are easily distinguished in dissection. *M.sexta* are sturdy and robust, with large larval and adult stages. These insects are sometimes referred to as the white lab rat of the entomology field [19].

### 3.1 The Thorax

The body of *M.sexta* is composed of three main sections common to any insect: the head, thorax, and abdomen (Fig. 3.b). The head contains the brain, two large compound eyes, and the coiled proboscis, used for feeding on plant nectar. The abdomen contains most of the organs related to digestion, reproduction, and circulation. Between them, the thorax serves as a powerhouse for muscular activity related to locomotion.

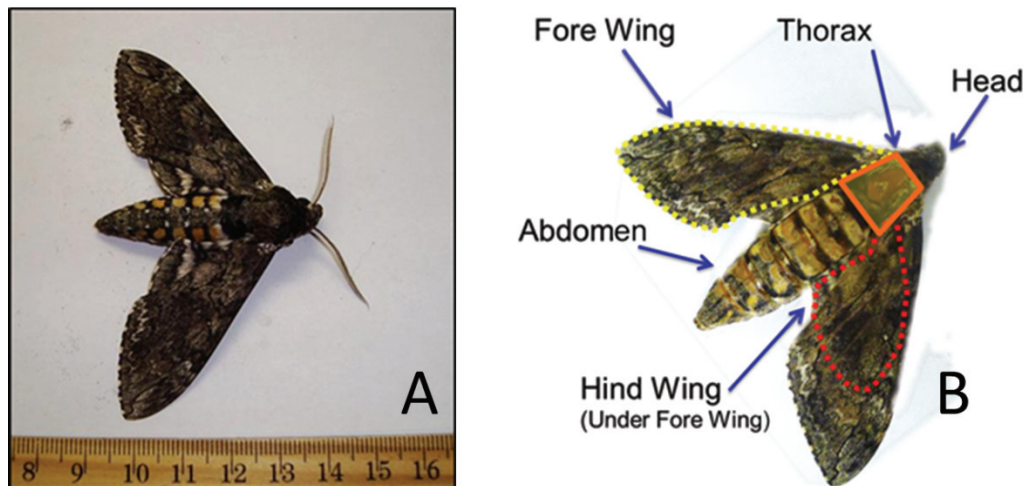


Fig. 3. (A) Dorsal view of *M.sexta* (scale is in centimeters), (B) Major body components

### 3.2 Flight Muscles

All four wings and all six legs protrude from the thorax and are controlled by the muscles therein. Therefore the thorax is the prime area of interest for research centered on power generation and the mechanical nature of power transfer related to flight. Fig. 4.a shows a cross-section of the thorax of *M.sexta*.

There are two large muscle groups in the thorax that indirectly control the flapping motion. These muscles do not act directly on the wing, instead, they push and pull on the thoracic exoskeleton which transfers energy to the wings through a complex hinge system. The powerful, lift-inducing downstroke is caused by the contraction of the dorsolongitudinal muscles (DLMs) (nomenclature after Eaton, [48]) which span the length of the thorax along the inner surface of the tergum (or tergal plate), which is the large plate of the exoskeleton on the top side of the thorax (Fig. 4.b).

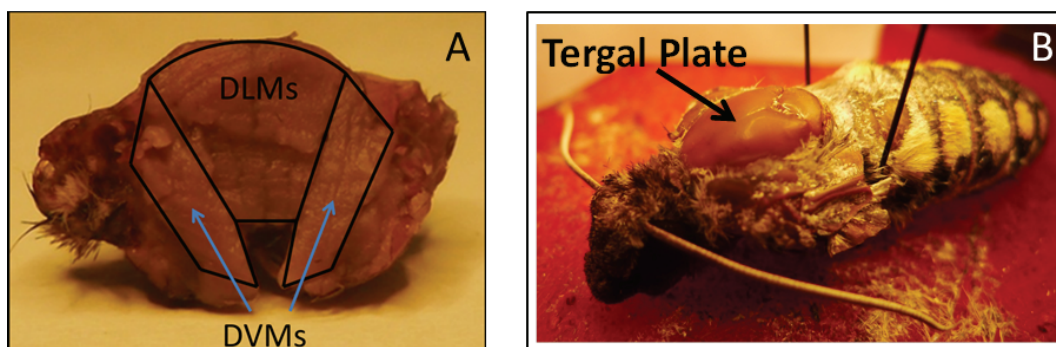


Fig. 4. (A) Hawkmoth flight muscles: Photograph of flight muscles in cross-section of thorax, (B) View of tergum with scales removed

The DLMs are attached to phragma at the front and rear of the thorax and their contraction bows the tergum upward, bringing the inner hinge of the wing with it, which quickly and efficiently swings the wings downward to a maximum displacement of about 30 degrees below horizontal in hovering flight [21]. The wings are similarly elevated by the contraction of the dorsoventral muscles (DVMs) which span vertically, at a slight angle, from the left and right sides of the tergum to the center of the sternum. Contraction of these muscles vertically compresses the thorax and lowers the inner hinge at the base of the wings, raising the wings to a maximum angle of approximately 65-75 degrees above horizontal during hovering flight [21]. Fig. 5 shows a schematic of these flight muscles in action:

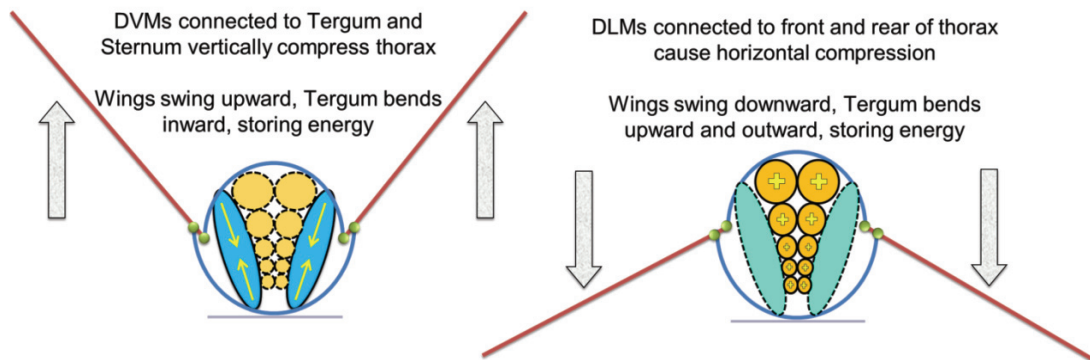


Fig. 5. Schematic of the indirect flight muscles of *M. sexta* in action

### 3.3 The Exoskeleton

*M. sexta*, like all insects, has its structural support on the outside of the body in the form of an exoskeleton, or cuticle. The exoskeleton of flying insects must be lightweight and efficient while still resilient enough to provide protection from predators and the elements. The cuticle is a composite of extremely strong, high-modulus crystalized chitin nano-fibers bound by a soft protein matrix along with small quantities of polyphenols and lipids [[22],[23]]. Water is also present in the cuticle and influences the material properties by acting as a plasticizing agent [24]. The cuticle, in one form or another, makes up nearly every outer part of an insect, including wings, shells, structural stiffeners, veins and joints.

In *M. sexta*, as with any insect with an indirectly-powered flight system, the thorax almost certainly absorbs and returns significant amounts of inertial energy with each wing beat [1,16]. The rapid movement of the wings swing from their natural upper or lower extremes produces large quantities of kinetic energy. At each extreme wing position, this kinetic energy must be counteracted as the wing is slowed and the direction of movement is reversed. If the thorax consisted of a rigid-joint system, with no provision to store this excess energy, the flight muscles would be required to provide all of the energy necessary for deceleration and acceleration. This would represent a major inefficiency in the flight mechanism and, as will be shown in the literature review, would probably require more power than these muscles are capable of producing. Therefore, the entire muscle/cuticle/wing system likely makes use of the energy-storing ability inherent in elastic materials and composites. It is also apparent that the insect flaps at or near the resonant frequency of the system, a quality which indicates, as expected, that flapping efficiency is ideal for flight [25]. Because the tergum is the largest single piece of the thoracic exoskeleton, and bends significantly during flight, it is seen as a crucial component whose mechanical properties are of interest. The elastic modulus of this component found by nanoindentation may be used in the future for mechanical energy storage calculations as well as Finite Element (FE) modeling.

## 4. LITERATURE REVIEW

Engineers can benefit from researching the historic and recent work regarding the topics of interest in the area of FWMAV research. This paper outlines three key subjects pertinent to this investigation. The first is one which is currently underutilized in FWMAV design: finite element modeling of biological components and systems. Next, nanoindentation for determining material properties is discussed.

Particular attention is paid to the use of nanoindentation to investigate biological materials. The value of examining insect cuticle as an engineering material is also explained in depth. Finally, the various aspects of power production, measurement, and calculation will be discussed as they relate to previous research and analyses of flying insects.

#### 4.1 Finite Element Modeling of Biological Systems

The concepts behind the FE method have been employed in various forms since the 1940's, though the term "finite element" was not coined until 1960 [24,26]. The original method allows simple structural calculations regarding stress and strain to be performed by hand for basic structural problems, but any practical applications require the computational power of a computer. Advancements in computer technology have led to a surge in FE analysis using ever-improving software programs. A biological organism is extremely complex and cannot be accurately modeled without the use of these highly advanced FE analysis techniques. Researchers have only recently undertaken to model components or subsystems of various biological organisms [27].

Few FE models of insect components have been created. In 1998, before the advent of highly-powerful FE modeling technology, a code was written for modeling a portion of a cockroach exoskeleton [28]. More recently, members of the FWMAV research effort at AFIT have created and analyzed FE models of *M.sexta* forewings [29,30].

Norris examined the mode shapes of the forewing (Fig. 6) [30]. That work was subsequently expanded with the creation of an improved model of the forewing (Fig. 7) and comparison of its results to the performance of an actual *M.sexta* forewing as it "flapped" through a natural range of motion on a flapper device [29].

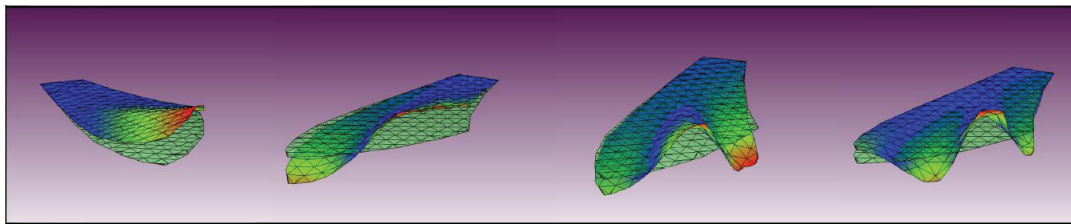


Fig. 6. Mode shapes of *M.sexta* forewing as modeled by Norris [30]

Recently, Chakravarty and Albertani developed a method for analyzing a hyperelastic latex membrane used on FWMAV wings with FE analysis [31]. They were able to successfully model the deformation and energy absorption behavior of this synthetic membrane and compare it to experimentally derived values. Although their technique was applied to manmade materials it is possible that it could be extended to biological wing membranes in the future.

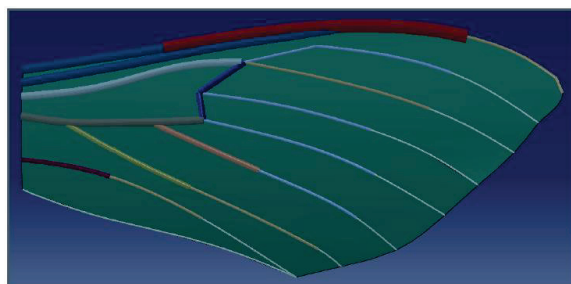


Fig. 7. Finite element model of *M.sexta* forewing by Sims et al. [29]

Researchers have recently devised mathematical models of an insect thorax [25]. However, an extensive search of the literature has turned up no evidence of FE models of a complete thorax. The first author developed what is most likely the first FE model of the *M.sexta* thorax in the spring of 2011 as a precursor to the present work [49]. The primary goal was to create a model which would provide insight into the function of the wing hinge. Effort was made to use realistic dimensions despite the

inherent geometric simplifications of the model. Fig. 8 shows a cross-section of an *M.sexta* thorax overlaid by a cross-section of the model. The lower half of the thoracic exoskeleton, consisting of the sternal and pleural plates, was modeled as a braced structure because it is much stiffer than the tergal plate and does not bend significantly during flight [25]. The first iteration involved this geometry being extended back for a few centimeters, essentially creating a “slice” of the thorax (Fig. 9.a). An improved model incorporated a 3-dimensional taper more closely resembling actual thoracic geometry (Fig. 9.b).

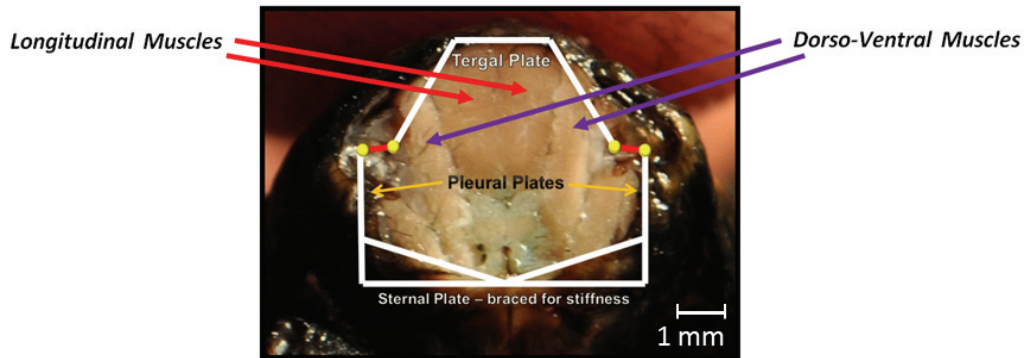


Fig. 8. Specimen cross-section and finite element model geometry overlay

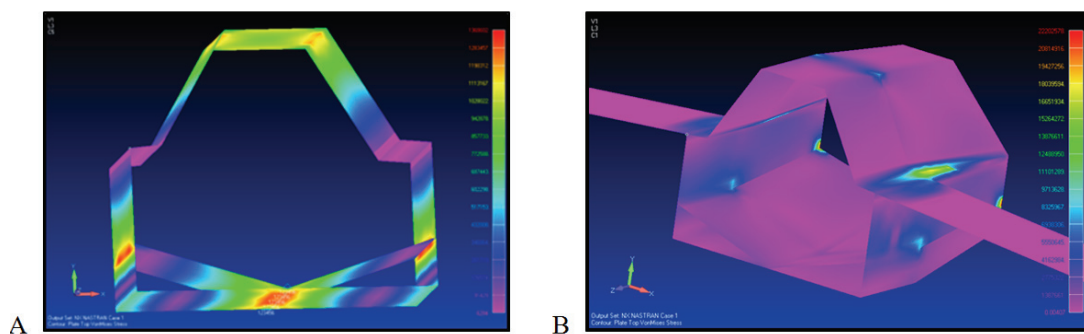


Fig. 9. FE models — (A) First model, thin extruded 2D shape, (B) Final model, 3D shape. The elastic modulus and the thickness of the elements were not realistic in these models. The location, not the value, of the stress concentration is the primary interest. [49]

Simplifying assumptions about the hinge allowed the production of a functional model. *M.sexta*, like all flying insects, has a resilin-filled pad of low-modulus, rubber-like cuticle separating the wing base from the hard plates of the thoracic body. This is the same material that stretches and compresses to store much of the elastic forces resulting from the inertia of the flapping wing [32]. These highly complex hinge regions contain small, tanned cuticle plates called *sclerites*, to which the small flight control muscles attach. These small muscles make fine adjustments to wing position for stability and control and do not provide significant lift. The simplified nature of this FE model dictated that the sclerites were left out. The hinge regions were modeled by applying low-modulus (several orders of magnitude lower than that of the body/wing material) properties to the finite elements on either side of the wing base (Fig. 10).

These models resulted in a better understanding of the interaction between the thorax and the wings. Fig. 11.a shows the model in an undeformed position before the application of a vertical compressive force on the tergam. Fig. 11.b shows the deflection caused by the application of a distributed downward force on the tergam, simulating the action of the DVMs. Fig. 11.c shows the position of the wings during the force application.



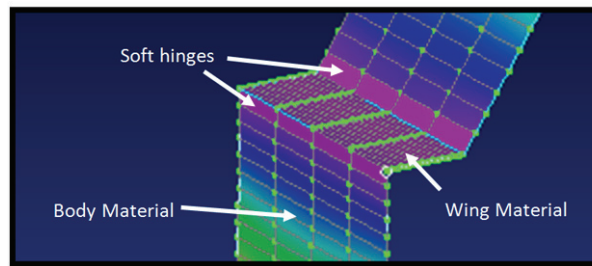


Fig. 10. Wing hinges modeled as soft (low modulus) material [49]

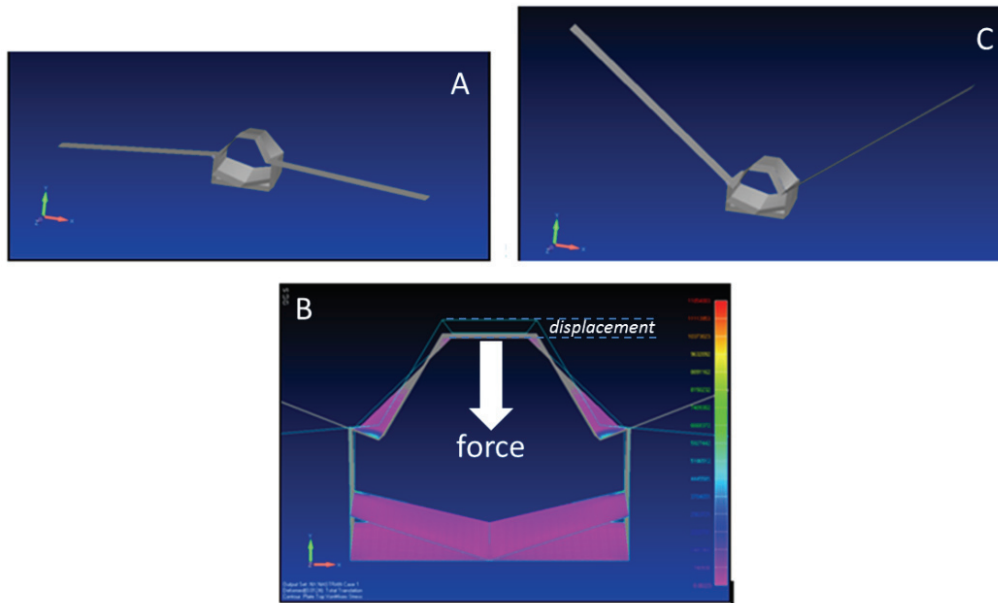


Fig. 11. Realistic wing deflection in FE model — (A) Undeformed, (B) Application of force representing DVMs, (C) Resultant wing elevation [49]

Power measurements and investigations of material properties will be applicable to future finite element models of the *M. sexta* thorax and of insect flight systems in general. Force and power data may eventually be applied to dynamic models, and the elastic modulus and thickness of the tergum and the rest of the thoracic cuticle is especially important for accurate modeling

#### 4.2 Nanoindentation for Elastic Modulus of Biological Materials

Nanoindentation has its roots in the concept of determining material hardness by scratching one material with another, a concept first described by Moh's scale of hardness. Eventually, mathematical solutions concerning the stress state of a hard material pressing into a softer material came along as more sophisticated experiments were developed [33]. Vickers, Knoop and Brinell are all measures of hardness that stem from the concept of indentation for determining material properties.

Useful results from nanoindentation experiments require measurement of extremely small forces and displacements with great accuracy and sensitivity. In 1992, Oliver and Pharr pioneered the effective use of a very small-scale version of the standard indentation test [34]. Nanoindentation had been around for a decade at that point, but the results had not been as precise or repeatable as other, more established methods for testing material properties. One of the most significant contributions of their work was the realization that the unloading curve was not linear, as had previously been assumed (Fig. 12).

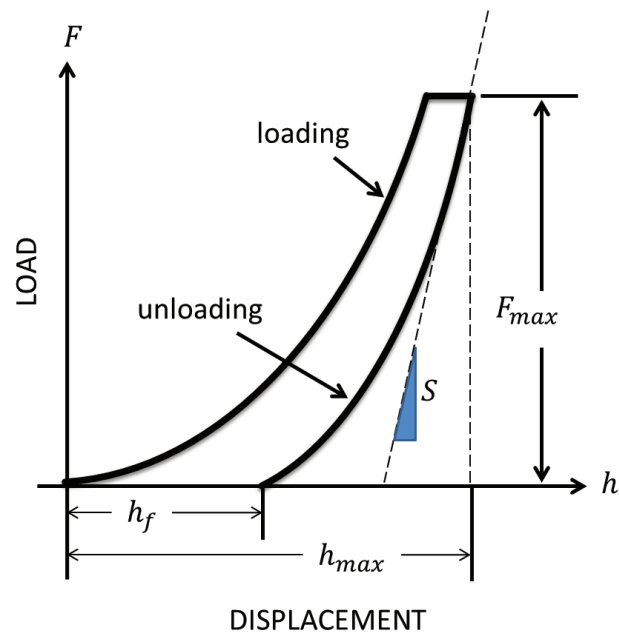


Fig. 12. Schematic of load versus indenter depth into surface for an indentation experiment.  $F_{max}$ : indentation load;  $h_{max}$ : indenter displacement at peak load;  $h_f$ : the final depth of the contact impression after unloading; and  $S$ : initial unloading slope.

#### 4.2.1 Nanoindentation of Insect Cuticle

The mechanical properties of the insect cuticle material have long been of interest. As the most structurally significant component of an insect's body, the cuticle is an engineering marvel with a diverse list of functions:

*“[T]he cuticle...has to perform all the functions of a skin and a skeleton, and that at low weight. The cuticle is, preternaturally, multifunctional: it not only supports the insect, it gives it its shape, means of locomotion, water-proofing and a range of localized mechanical specializations such as high compliance, adhesion, wear resistance and diffusion control. It can also serve as a temporary food store and is a major barrier to parasitism and disease.” [22]*

Engineers can look to insects to gain valuable knowledge about functional integration, which is especially applicable in the world of MAV design. The various sensors, flight controls, energy sources and circuitry will all need to be integrated into a small package with enough room left over for a payload. It currently seems unlikely that all of these components can be designed to fit in or on a stand-alone fuselage that is not integrated with these functions. Additionally, provisions for inertial energy storage during flapping will probably be necessary, as it is apparent that most large insects would not be able to fly without inertial power storage [35]. Understanding how *M.sexta* accomplishes functional integration and inertial power storage will aid engineers' efforts at designing an effective FWMAV.

The relation of the flight of a locust to the mechanical properties of its cuticle had been investigated long before the advent of nanoindentation [32]. Though it was well-acknowledged that elasticity of the cuticle plays at least a partial role in insect flight, no relevant research had been done prior to Jensen and Weis-Fogh regarding the elastic properties of any arthropod cuticle. These researchers used tensile and compressive tests to examine both the hard cuticle and the soft, rubber-like cuticle of a locust, arriving at an elastic modulus for the hard material of between 8 and 10 GPa, consistent with modern data.

Although these researchers were able to obtain accurate results, the use of nanoindentation could have streamlined their research. More modern studies have already made use of this technique for examining the material properties of the cuticle. A few of these studies have focused on the specialized cuticle which forms the articulating joint between the thorax and the head of the beetle *Panchnoda*

*marginata* [36,37]. These efforts produced significant insight into the effects of desiccation on the hardness and elastic modulus of insect cuticle. The hardness and modulus of that highly-flexible, low-modulus articulating cuticle both increased significantly with desiccation. Water had comprised 15-20 percent of that component's mass prior to drying. It is interesting to note that the elastic modulus of the fresh cuticle was found to be 1.5 GPa, which is much lower than the modulus of *M.sexta*'s tergum at 5 GPa [50]. It is likely that the hinge material at the base of *M.sexta*'s wings exhibits similar material properties to the *P.marginata* articulation cuticle.

### 4.3 Power Estimation and Measurement

Another branch of investigation, of both engineering and biological interest, involves the study of the actual and/or theoretical power output of an insect in hovering flight. Flapping flight is more energetically demanding than the standard fixed-wing variety with which aeronautical engineers are most familiar. The demand for actuators with a high power density is further reinforced by the weight and size constraints of a FWMAV. Evaluations of the power requirements of natural flappers like *M.sexta* provide an order-of-magnitude goal for FWMAV developers. Methods for calculating and measuring energetic input and output of flying insects have been around since the 1970's, while research on the energetic properties of the flight muscles dates back to at least 1956 [38,16]. Mechanical power output ( $P_{o,m}$ ) is defined as the sum of the *inertial power* ( $P_{o,i}$ ) and the *aerodynamic power* ( $P_{o,a}$ ) required for hovering flight.  $P_{o,i}$  is the power needed to oscillate the wings through each wingbeat, though the actual net value depends on the amount of elastic storage present [2]. Perfect elastic storage means that there will be no inertial power requirement ( $P_{o,i} = 0$ ).  $P_{o,a}$  can be further broken down into profile, induced, and parasite power, which are detailed in [16] and will not be examined here. Fig. 13 shows the energy expenditure pathway of a flying insect [16].

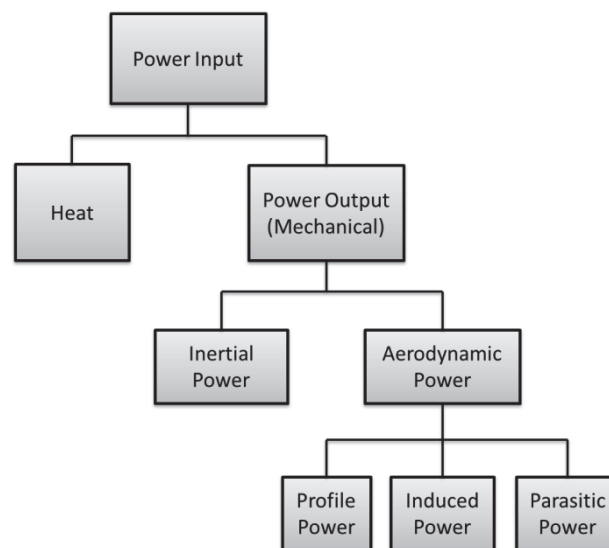


Fig. 13. Pathway for energy expenditure of a flying insect. The inertial power is required to overcome the momentum of the wings in order to flap. The aerodynamic power is the combination of all aerodynamic forces against the movement of the wings. Parasitic power is negligible for hovering. Induced power accelerates the air through the wing disc. Profile power overcomes the wing drag. (after Casey, [16])

Theoretically, if all of the energy from the rotating wing mass is stored in the stretching flight muscles and bending thoracic exoskeleton, then we can say there exists perfect elastic storage. In this case the mechanical power is simply equivalent to the aerodynamic power requirement:  $P_{o,m} = P_{o,a}$ . On the other extreme, zero elastic storage would mean the wings would have to be slowed down, stopped, and accelerated at each half-stroke maximum by the action of the flight muscles alone, which would greatly increase the total mechanical power output required in large flyers like *M.sexta*. The reality is that elastic storage lies between these two extremes [2].

$P_{o,m}$  can also be estimated by dividing the required metabolic power input ( $P_i$ ) by the muscle efficiency ( $E_m$ ). Estimates for muscular efficiency in insects are based on measurements of oxygen

consumption which can be related to energy expenditure and compared with the measured or estimated mechanical power output. The metabolic power input requirement for *M.sexta* in hovering flight has been reported as  $237 \text{ W}\cdot\text{kg}^{-1}$  body mass [39] and  $1170 \text{ W}\cdot\text{kg}^{-1}$  muscle mass [42]. Ellington used this method and the aerodynamic/inertial summation and compared the  $P_{o,m}$  results to gain insight into the nature of the elastic storage [16].

Ellington then concludes that the evidence for elastic storage is high, which meant that the efficiency of the flight muscles was much lower than previously thought, around 5-8 percent assuming perfect elastic storage. That value increased to 11-17 percent if elastic storage was entirely neglected. Previously accepted values for insect muscle efficiency were between 20 and 30 percent [2]. However, other estimates of the power output of insect muscle, based on the wingbeat frequency, have been set forth. These researchers directly studied the physical construction of muscle fibers and were able to correlate the specific power output with the contraction frequency, which is the same as the flapping frequency for insects like *M.sexta* that have synchronous muscle fibers. Their method yields an estimated power output of approximately  $82\text{-}97 \text{ W}\cdot\text{kg}^{-1}$  (muscle mass) for *M.sexta*, whose wingbeat frequency is between 25 and 30 beats per second [40]. Their higher estimation of power output meant that  $E_m$  for insect flight muscle would be between 11 and 17 percent with perfect elastic storage [2].

Mechanical work output of the major flight muscles in *M.sexta* has also been measured using a work loop technique first developed by Machin and Pringle and later adapted for synchronous muscles like *M.sexta*'s by Stevenson and Josephson [41,42]. Using electrical stimulation and an imposed sinusoidal length change, Stevenson and Josephson determined that the DVMs of *M.sexta* produce an average maximum power output of  $90 \text{ W}\cdot\text{kg}^{-1}$  at a temperature range of 35-40 °C. This measurement fits well with the rest of the data available for power output of insect muscle as well as with the ideal internal thoracic temperature of *M.sexta*'s thorax during flight. A more recent experiment using a similar approach arrived at an average maximum power output of  $83.3 \text{ W}\cdot\text{kg}^{-1}$  for the DLMs [43]. This is consistent with previously measured and estimated values.

Advancements in high-lift generation at low Reynolds conditions have led to increasingly accurate predictions of power requirements in insect flight [44]. The theory of unsteady high-lift fluid mechanics is described in Sun's paper and will only be briefly mentioned here. Basically, delayed stall, in the form of leading edge vortices held attached by span-wise flow, works as the high-lift device for flapping wings of insects. Pronation and supination of flexible wings can also create rotational circulation and wake capture which creates aerodynamic forces during stroke reversals [51].

Sun and Du computed the specific power requirement of 8 insect species, ranging from fruit fly to hawkmoth, by numerically solving Navier-Stokes equations [1]. They arrived at a power output for *M.sexta* of  $39 \text{ W}\cdot\text{kg}^{-1}$  (body mass) without elastic storage and  $33 \text{ W}\cdot\text{kg}^{-1}$  with elastic storage. For a *M.sexta* specimen with flight muscles comprising 20% of body weight [42], these values correlate to approximately  $164$  and  $194 \text{ W}\cdot\text{kg}^{-1}$  (muscle mass) respectively, which is slightly higher than the previous data. They concluded that large insects like *M.sexta* benefit greatly from elastic storage, because a large portion of this power requirement was due to inertial force from the wings [1].

Liu and Aono studied the low-Reynolds hovering of insects using a computational method in 2008. They were able to use their data to arrive at a power output of  $39.5 \text{ W}\cdot\text{kg}^{-1}$  (body mass) for a different species of hawkmoth (*Agrius convolvuli*) [45]. Their value is based on the aerodynamic power, having calculated that the inertial power is minimal. This conflicts with Sun's and Du's results regarding inertial power, which they found to be about  $6 \text{ W}\cdot\text{kg}^{-1}$  or about 20% of aerodynamic power.

Most recently, Zhao and Deng have investigated the aerodynamic and inertial power distribution in *M.sexta* [46]. Known hovering kinematics were combined with forces and torques measured with model hawkmoth wings to calculate the power values. They determined that inertial power requires nearly half of the total power expenditure assuming zero elastic storage. The specific power was determined to be  $19.7 \text{ W}\cdot\text{kg}^{-1}$  (body mass) and  $16.4 \text{ W}\cdot\text{kg}^{-1}$  for aerodynamic and inertial forces, respectively. This means that if *M.sexta* stores a large portion of this inertial power with elastic action, the power output should be close to  $20 \text{ W}\cdot\text{kg}^{-1}$  (body mass) or  $100 \text{ W}\cdot\text{kg}^{-1}$  (muscle mass). If the moth must overcome all inertial forces, these results require a power output of  $36.1 \text{ W}\cdot\text{kg}^{-1}$  (body mass) or  $180 \text{ W}\cdot\text{kg}^{-1}$  (muscle mass). All of the power output and input (consumption) values reported in this paper are summarized in Table 1.

Table 1 - Summary of power density estimations for the hawkmoth *M.sexta*. Some researchers reported their results as power per body mass. These have been converted to power per muscle mass by assuming a flight muscle to body ratio of 20% [19]. The power per muscle mass numbers indicated in bold font are the most pertinent values for this study, as they have been obtained directly from analyses of the flight muscles. Power input is also presented below. Stevenson and Josephson report power consumption based on metabolic analysis of the hawkmoth in flight and the 20% flight muscle to body mass ratio. Theirs is likely the most accurate power input value.

<b><i>M.sexta</i> Power Output</b>		<b>specific power (<math>W \cdot kg^{-1}</math>)</b>		<b>notes</b>
<b>researcher/year</b>	<b>method</b>	<b>body mass</b>	<b>muscle mass</b>	
Casey 1976	estimation from power input	41-54	*205-270	Based on measurements of power input and estimate of 20% efficiency. We now know that actual efficiency is much lower
Pennycuik, Rezende 1983	muscle study	-	<b>82-97</b>	Estimated power density of muscle based on a known value for power density of mitochondria
Stevenson, Josephson 1990	work-loop	-	<b>90</b>	Mean maximum power. Absolute max reached 130 in two specimens. 50-80 determined to be min. power req'd for flight
Sun, Du 2003	numerical	33-39	*164-194	With elastic storage - without elastic storage
Tu, Daniel 2004	work-loop	-	<b>83.3</b>	Specifically studied the DLMs
Liu, Aono 2009	computational	39.5	*197.5	Diff. species of hawkmoth, <i>Agrius convolvuli</i>
Zhao, Deng 2009	kinematics and aerodynamics	19.7 (aero) 16.4 (inertial)	*98-180	With elastic storage (no inertial power) - Without elastic storage (must overcome all power requirements)
Hollenbeck 2012	mechanical	-	<sup>†</sup> <b>72-143</b>	Direct measurement of mechanical power

\*indicates equivalent value based on 20% muscle mass

<sup>†</sup>estimated range based on DVM/flight muscle ratio of 15% - 30%

<b><i>M.sexta</i> Power Input</b>		<b>specific power (<math>W \cdot kg^{-1}</math>)</b>		<b>notes</b>
<b>researcher/year</b>	<b>method</b>	<b>body mass</b>	<b>muscle mass</b>	
Casey 1976 (Reporting Heinrich 1971)	metabolic	191-289	478-722	Moth flies in closed jar and depletion of oxygen is measured/correlated to energy by assuming fat utilization during flight
Casey 1976	metabolic	237	694	Based on oxygen consumption
Stevenson, Josephson 1990	metabolic	-	<b>1170</b>	Derived from Heinrich's $O_2$ consumption. Most reliable number based on newer data

## 5. CONCLUSION

This paper presents a review of existing literature regarding three approaches to the mechanical investigation of a biological system for FWMAV engineering applications. Finite element modeling, nanoindentation and power calculations can each provide insight into the mechanism of hovering flight in insects. All three of these areas of research can potentially yield increasingly useful data as the scope of their use and their methods improve. Recently, the first author's research [50] yielded a mechanical power output of 80-120  $W \cdot kg^{-1}$  muscle mass for *M.sexta*. In addition, nanoindentation has yielded an elastic modulus of 5 GPa for the tergal plate and the static response of the flapping mechanism has been characterized. The modulus and static response are currently being used in the creation and validation of finite element models of this mechanism [52].

## ACKNOWLEDGEMENTS

The views expressed in this article are those of the author and do not reflect the official policy or position of the United States Air Force, Department of Defense, or the U.S. Government. The authors would like to thank Dr. Douglas Smith of the Air Force Office of Scientific Research for financially supporting this research.

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